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Echinoderes aureus n. sp. (Kinorhyncha: Cyclorhagida) from Tanabe Bay (Honshu Island), Japan, with a Key to the Genus *Echinoderes*

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A new species of echinoderid kinorhynch, *Echinoderes aureus*, is described and illustrated using a differential interference contrast microscope with Nomarski optics. The kinorhynchs were collected from washings of a brown alga, *Padina arborescens* Holmes, growing in tide pools in Tanabe Bay, Honshu Island, Japan. Diagnostic characters of *E. aureus* are the presence of middorsal spines on segments 6–10, lateral spines/tubules on segments 4 and 7–12, a pair of remarkably large subcuticular scars in a subventral position on segment 3, and an incomplete midventral articulation on segment 4. The positions of numerous sensory-glandular organs, the sizes of various lateral spines/tubules, and the shapes of the terminal tergal and sternal extensions are also diagnostic. *Echinoderes aureus* constitutes the 59th valid species of the genus *Echinoderes* and the 15th species described from the Pacific Ocean. This is the fourth representative of Pacific kinorhynchs found only in the intertidal zone and the second Pacific *Echinoderes* living on macroalgae in tide pools. A dichotomous key to all 59 species is provided.

Key Words: kinorhynch, taxonomy, *Echinoderes*, key, placid, spine, tubule, setae

Introduction

Kinorhyncha constitutes a taxon of meiobenthic, free-living, segmented and spiny marine invertebrates, generally less than 1 mm in length. Previously, the taxon had been considered a class of the phylum Aschelminthes (Hyman 1951), but it was subsequently regarded as currently considered an independent phylum with close relationships to aschelminth worms (Higgins 1971; Kristensen and Higgins 1991). Recently, the Kinorhyncha has been included as a class of the phylum Cephalorhyncha (Adrianov and Malakhov 1994, 1999) and the group Aschelminthes has been considered polyphyletic or paraphyletic (Ahlrichs 1997; Kristensen and Funch 2000).

According to the last taxonomic review of the Kinorhyncha (Adrianov and Malakhov 1999) and subsequent recent descriptions (Sørensen *et al.* 2000; Adrianov *et al.* 2002), the genus *Echinoderes* consists of 58 valid species, 14 of which have

been reported from the Pacific Ocean.

A few studies, mostly dealing with the ecology of subtidal meiofauna, have reported the presence of kinorhynchs in Japanese waters. The first record of Kinorhyncha from Japan was "*Echinoderes* sp." in Kawamura (1927), collected by Taku Komai in 1925 at the Misaki Marine Biological Station near Tokyo (Kawamura 1927, 1947; Tokioka 1949). Abe (1930) later described a new species, *Echinoderes masudai* Abe, 1930, found at Gogoshima Island near Matsuyama. The description of the species was, however, too poor to allow comparisons, and *E. masudai* is not currently regarded as a valid species, rather as a *species indeterminata* (Higgins 1983; Adrianov and Malakhov 1999). Tokioka (1949) reported another species of *Echinoderes*, *E. dujardinii* Claparède, 1863, from Ago Bay, Honshu Is. Some years later, this species was listed by Sudzuki (1976a, b) from meiobenthic samples around Kasado Island in the Seto Inland Sea. Findings of *E. dujardinii* in Japan are highly questionable, though, because the species has been known only from European waters, and the reports of Tokioka (1949) and Sudzuki (1976a, b) seem likely to be misidentifications (Higgins 1983; Adrianov and Malakhov 1994). Quite recently, a new species, *Echinoderes sensibilis* Adrianov, Murakami and Shirayama, 2002, was described from the intertidal zone of Tanabe Bay (Honshu Island). This species constitutes the first valid species of the genus *Echinoderes* described in Japan to date (Adrianov *et al.* 2002). The present paper will describe the second species of the genus *Echinoderes* from Japan, and will be the fourth one of our series regarding taxonomic study of the Kinorhyncha in Japan.

The first key to adults of *Echinoderes*, for the first eight described species, was published by Zelinka (1928). More than a half century later, Higgins (1983) published a modern key including the 38 valid species of *Echinoderes* known to that time, along with the standard protocol for examination procedures that is now accepted by most kinorhynch taxonomists. Higgins and Kristensen (1988) then published a new key for 44 valid species of *Echinoderes*, and two other keys for the genus *Echinoderes* were published by Huys and Coomans (1989) and by Adrianov and Malakhov (1994), for 45 and 48 species, respectively. Quite recently, a key for 54 valid species of *Echinoderes* was published by Adrianov (see Adrianov and Malakhov 1999). Five additional species inclusive of the present species have been described since then (Pardos *et al.* 1998; Sørensen *et al.* 2000; Adrianov *et al.* 2002). This paper thus includes an updated key to the currently known valid species of the geuns.

Materials and Methods

Six adult specimens, three males and three females, of the genus *Echinoderes* were collected from washings of the brown alga *Padina arborescens* Holmes in March, 2001, from tide pool in Tanabe Bay, located on the coast of the Kii Peninsula of Honshu Island (33°42.2′N, 135°22.9′E) in the vicinity of the Seto Marine Biological Laboratory of Kyoto University (Fig. 1). All specimens were fixed in 10% buffered formalin in seawater. Specimens were transferred into a 70% ethanol-5% glycerol-25% deionized water solution. After letting the ethanol and water evaporate, the material was preserved in absolute glycerol. Three males and three females then were mounted individually in Hoyer's-125 mounting medium between

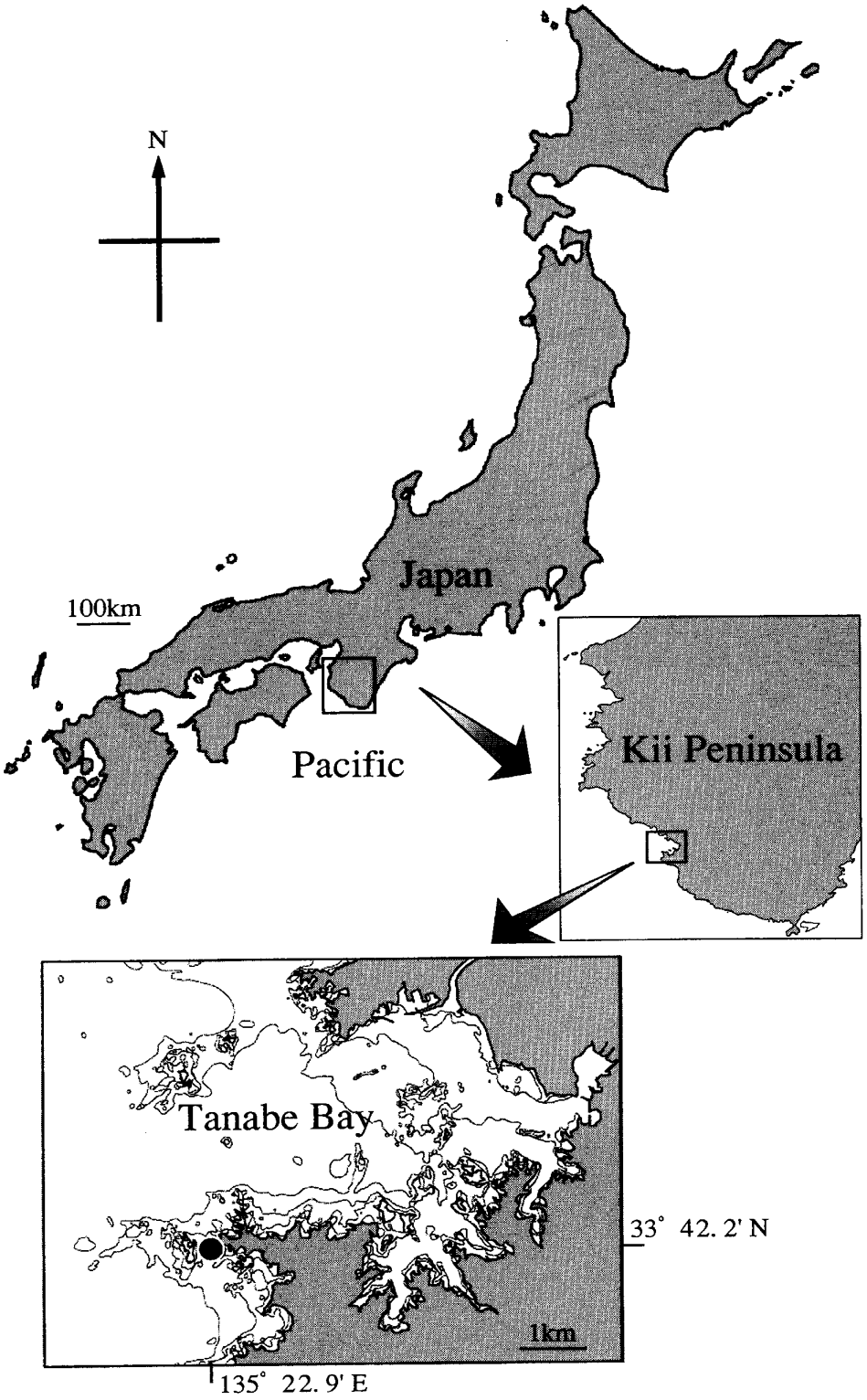

Fig. 1. Map showing the place (black circle) where *Echinoderes aureus* n. sp. was collected (Tanabe Bay, Kii Peninsula, Honshu Island, Japan).

two cover slips and positioned on Higgins-Shirayama plastic slide frames for further examination under a differential interference contrast microscope equipped with Nomarski optics.

We followed the standard protocol for examination described by Higgins (1983). Indices are expressed as percent of total length (TL) measured along the midline, from the anterior margin of segment 3 (first trunk segment) to the posterior margin of segment 13, exclusive of spines. Maximum sternal width (MSW) was measured at the anteroventral margin of the widest pair of sternal plates as first encountered in measuring each segment from anterior to posterior. Standard width (SW), or sternal width of segment 12, was measured at the anteroventral margin of the 12th sternal plates. Measurements are given for lengths of trunk segments (L), lateral terminal spines (LTS), lateral terminal accessory spines (LTAS), middorsal spines (DS), and lateral spines/tubules (LS). The locality data for the material examined refers to the collector's initials (AVA and CM). The specimens coded as CM have been deposited in the meiofaunal collection of the Seto Marine Biological Laboratory of Kyoto University, and those coded as AVA in the meiofaunal collection of the Institute of Marine Biology in Vladivostok, Russia.

In recording taxonomic characters such as the nature, location, and distribution of cuticular structures, we followed the reevaluated interpretation of dorsal, lateral, and ventral surfaces of the trunk that was proposed by Pardos *et al.* (1998, fig. 2). Detailed terminology used in this paper is mainly based on Higgins (1983), Pardos *et al.* (1998), and Adrianov and Malakhov (1999). Cuticular structures such as sensory spots, pore sieves, and glandular tubes are indicated in the text as "sensory-glandular structures" to avoid misinterpretation of characters studied only by light microscopy. As shown in Adrianov *et al.* (2002), these characters can be clearly distinguished only by scanning electron microscopy (SEM), which we were not able to use in this study because of the paucity of material.

Positions of cuticular structures on the trunk segments are indicated as follows: middorsal (MD)—on the middorsal line of the segment; paradorsal (PD)—adjacent to the middorsal line of the segment; subdorsal (SD)—lateral to the paradorsal position, closer to the middorsal line than to the maximum width of the segment; dorsolateral (DL)—on the dorsal surface, closer to the point of maximum width of the segment than to the middorsal line; midlateral (ML)—at the maximum width of the segment; sublateral (SL)—between the lateral accessory position (see below) and the midlateral position; lateral accessory (LA)—on the tergal plate ventrally adjacent to the sublateral position (position of lateral accessory spines/tubules); lateroventral (LV)—on the tergal plate adjacent to the tergal-sternal articulation (position of lateral spines/tubules); ventrolateral (VL)—on the sternal plate adjacent to the tergal-sternal articulation; subventral (SV)—on the sternal plate, between the midvental articulation of the sternal plates and the ventrolateral position.

Systematics

Order **Cyclorhagida** (Zelinka, 1896) Higgins, 1964
Suborder **Cyclorhagae** (Zelinka, 1896) Zelinka, 1928
Family **Echinoderidae** Bütschli, 1876
Genus ***Echinoderes*** Claparède, 1863
Echinoderes aureus n. sp.
(Figs 2–6)

Diagnosis. Incised anterior margin on basal plates of four trichoscalids centered above subventral and subdorsal placids; segment 3 with pair of large subcuticular scars in subventral position; segment 4 with incomplete, weakly developed midventral articulation; middorsal spines on segments 6–10 slightly shorter than length of corresponding segment; lateral spines/tubules on segments 4 and 7–12; lateral tubules on segment 4 equal in length to their segment; lateral spines/tubules on segment 12 longest, equal in length or slightly longer than lateral terminal accessory spines, in both sexes slightly shifted dorsally to midlateral position; lateral spines/tubules on segment 8 clearly shorter than other lateral spines; posterior margin of segments 9–11 with enlarged dorsal pectinate fringe; terminal tergal extensions (furcae) pointed, each with minute mesial projection; terminal tergite with prominent subdorsal pectinate fringe; lateral terminal spines 31–38% of trunk length.

Type locality. Tide pools, Bansyo-Zaki, Tanabe Bay, Kii Peninsula, Pacific coast of Honshu Island, Japan (33°42.2′N, 135°22.9′E) (Fig. 1). On brown alga, *Padina arborescens*.

Type material. Holotype, adult male (AVA-C-JAP-E01.2) (Fig. 2); allotype, adult female (CM-A-JAP-E03.2, SMBL Type No. 397) (Fig. 3); other paratypes, two adult males (AVA-C-JAP-E06.2; AVA-C-JAP-E10.2) and two adult females (AVA-C-JAP-E04.2; CM-A-JAP-E04.2, SMBL Type No. 398).

Etymology. From the Latin *aureus*, golden, alluding to the coloration of the cuticle.

Description. *Adult male* (Fig. 2). TL 277 μm; MSW-7 61 μm, 22% of TL; SW 60 μm, 21% of TL; LTS 106 μm, 38% of TL.

Segment 1 (head): enlarged basal plates of two subventral trichoscalids centered above subventral placids; basal plates of two subdorsal trichoscalids centered above subdorsal placids; all four basal plates with deeply incised anterior margins (Fig. 6A, white arrows, for female).

Segment 2 (neck): with 16 placids of various widths; midventral placid largest, 11 μm high, 6 μm wide at top, 11 μm wide at base; subventral placids 13 μm high, 7 μm wide at base; middorsal placid very narrow, 13 μm high, 5 μm wide at base; spaces between neighbouring placids with thin cuticular intermediate folds well seen in open closing apparatus.

Segment 3 (first trunk segment): 30 μm long, 56 μm wide along anterior margin; dorsal and ventral rows of subcuticular scars alongside anterior margin (Figs 4A, 5A, white arrowheads); two large, rounded subcuticular scars in subventral position (Fig. 4A, B, black arrowheads); one sensory-glandular structure in middorsal position (Fig. 5A, upper arrow); four pairs of sensory-glandular structures in subdorsal, dorsolateral, subventral, and ventrolateral positions.

Segment 4: length 32 μm, with pair of lateral tubules 29 μm long; incomplete,

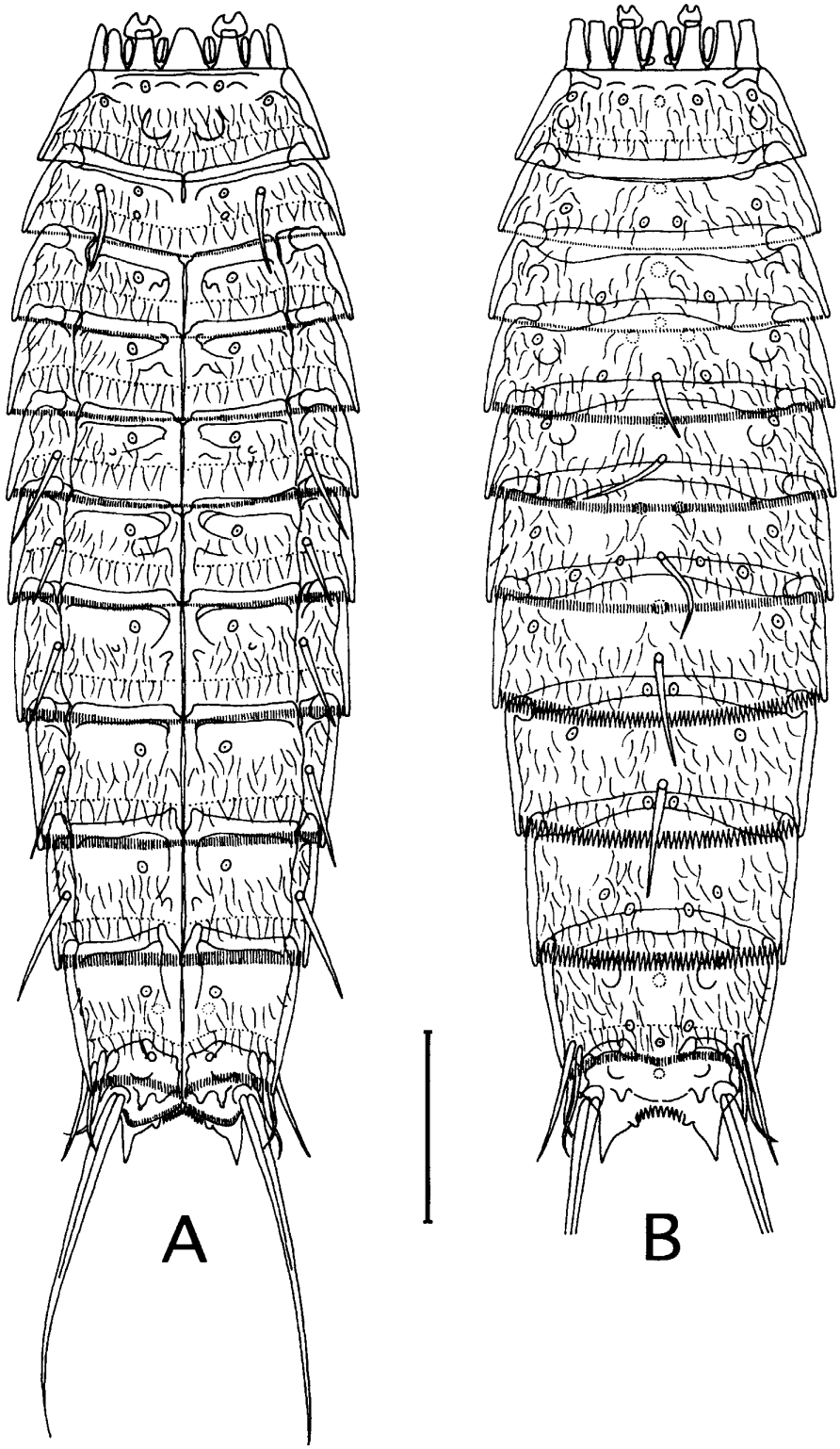

Fig. 2. *Echinoderes aureus* n. sp., holotype male. A, ventral view; B, dorsal view. Dotted circles, circles with a central dot, and plain circles indicate various sensory glandular structures. Scale bar=50 μm.

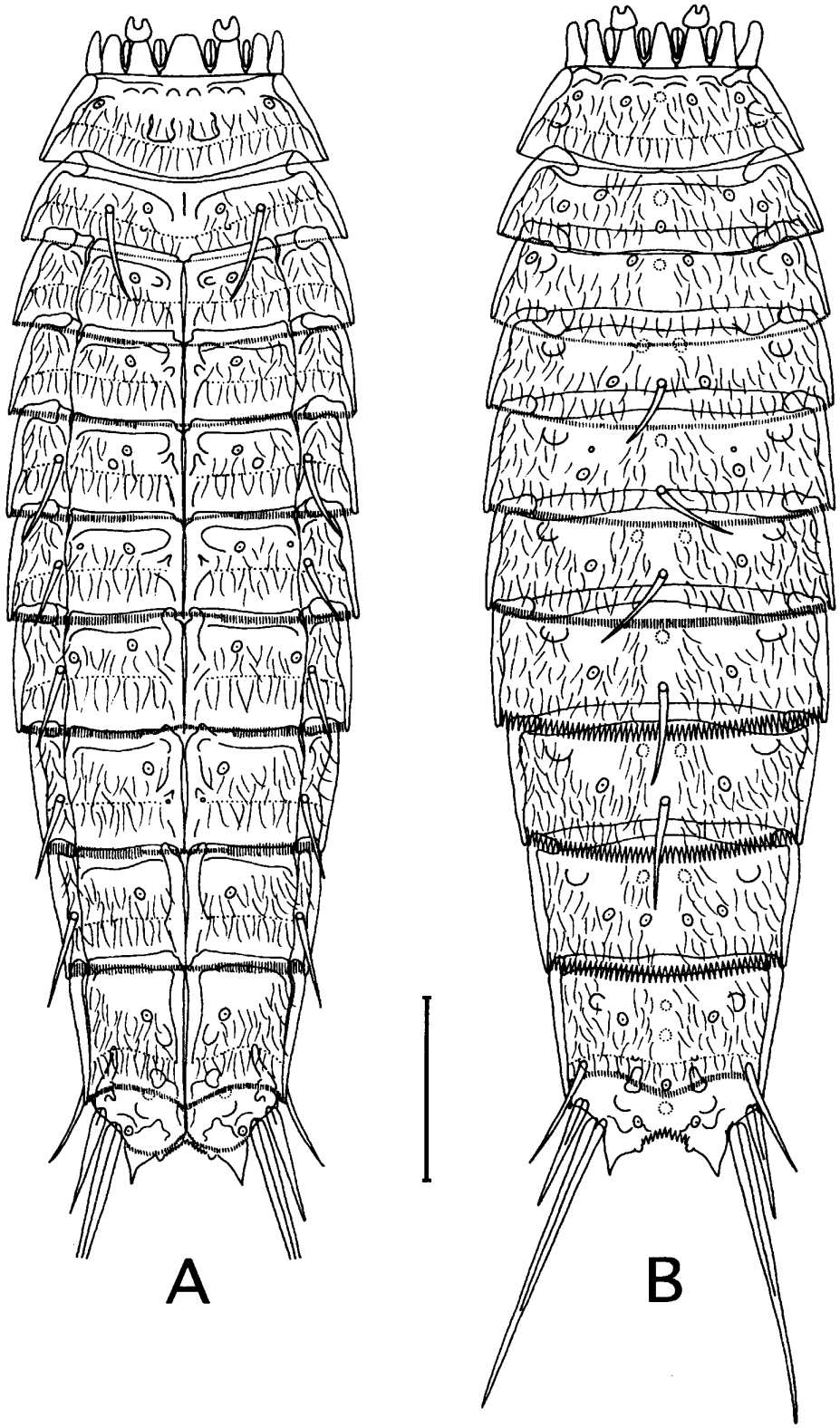

Fig. 3. *Echinoderes aureus* n. sp., allotype female. A, ventral view; B, dorsal view. Dotted circles, circles with a central dot, and plain circles indicate various sensory-glandular structures. Scale bar=50 μm.

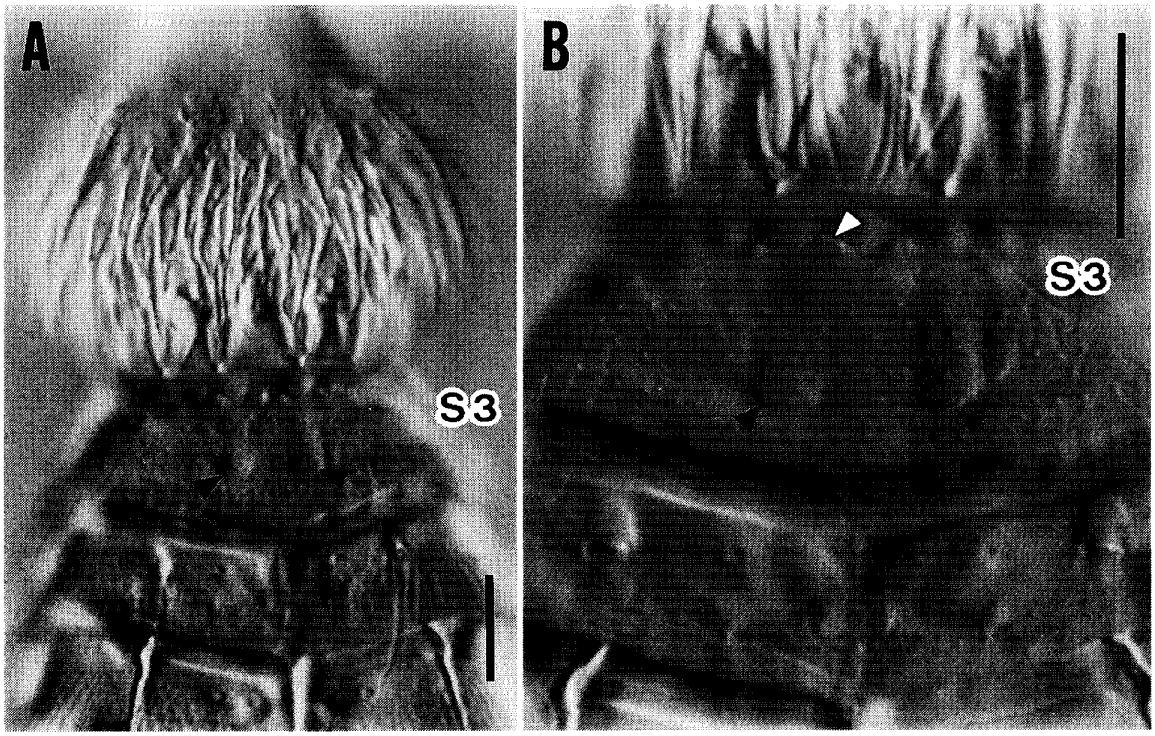

Fig. 4. *Echinoderes aureus* n. sp., A, B: holotype male, ventral view of anterior segments. Black arrow indicates weakly developed midventral articulation on segment 4; black arrowheads indicate large subcuticular scars in subventral position on segment 3 (S3); white arrowhead indicates subcuticular scars at anterior margin of segment 3. Scale bars=20 μm.

weakly developed midventral articulation visible only in anterior half of midventral pachycycli (Fig. 4B, arrow); posterior pectinate fringe undeveloped; one sensory-glandular structure in middorsal position (Fig. 5A, lower arrow); four pairs of sensory-glandular structures in paradorsal, dorsolateral, and subventral positions.

Segment 5: length 34 μm, with two sternal plates; maximum sternal width 47 μm; midventral pachycycli with lateral incisions; one sensory-glandular structure in middorsal position; two pairs of sensory-glandular organs in subdorsal and subventral positions; pair of large muscle scars (attachment of dorso-ventral muscles) in dorsolateral position.

Fig. 5. *Echinoderes aureus* n. sp., holotype male, dorsal view. A, segments 2–4; B, segments 12 (S12)–13. PF, posterior pectinate fringe of terminal tergal plate; TE, terminal tergal extensions. Black arrows indicate middorsal sensory-glandular structures; black arrowhead indicates subcuticular scar on terminal tergal plate; white arrowheads indicate subcuticular scars at anterior margin of segment 3 (S3). Scale bars=20 μm.

Fig. 6. *Echinoderes aureus* n. sp., allotype female, ventral view. A, segments 2–3; B, segments 12–13. PA, anterior ventral pachycycli of segment 13; SE, terminal sternal extension; TE, terminal tergal extension. Black arrow indicates lateral terminal accessory spine; black arrowhead indicates lateral tubules of segment 12 (S12); white arrows indicate basal plates of subventral trichoscalids; white arrowheads indicate subcuticular scars at anterior margin of segment 3 (S3). Scale bars=20 μm.

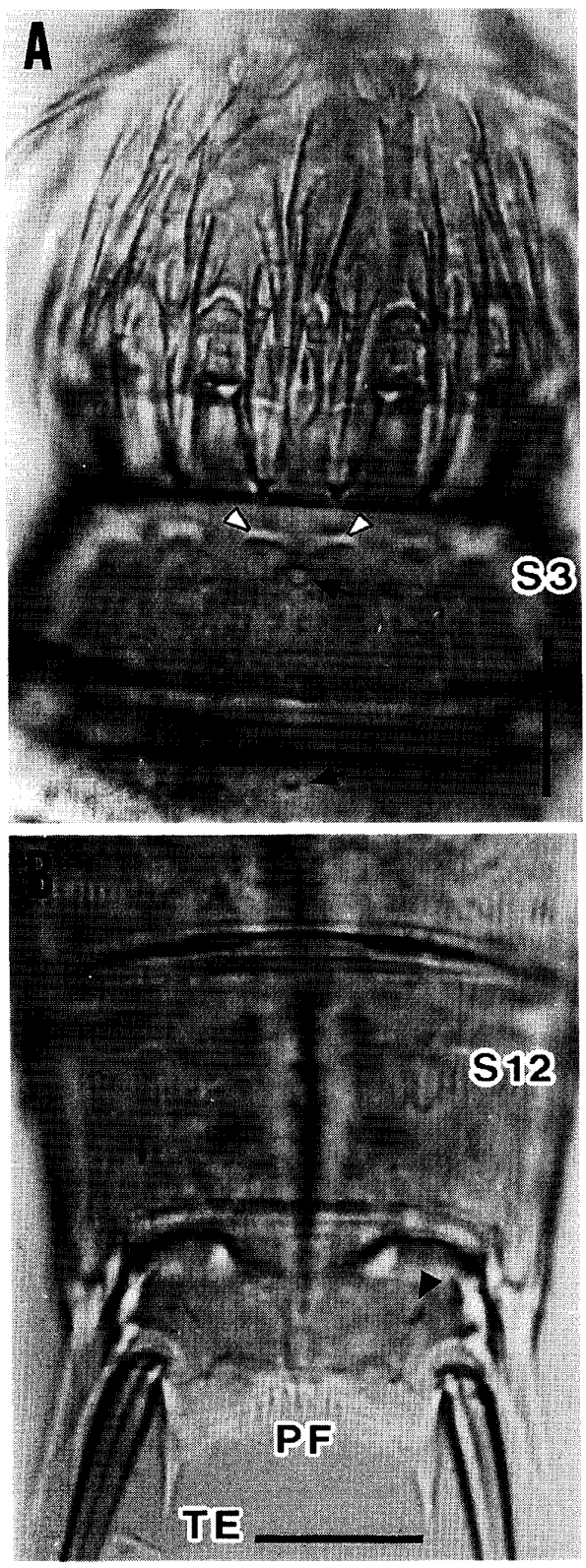

Fig. 5.

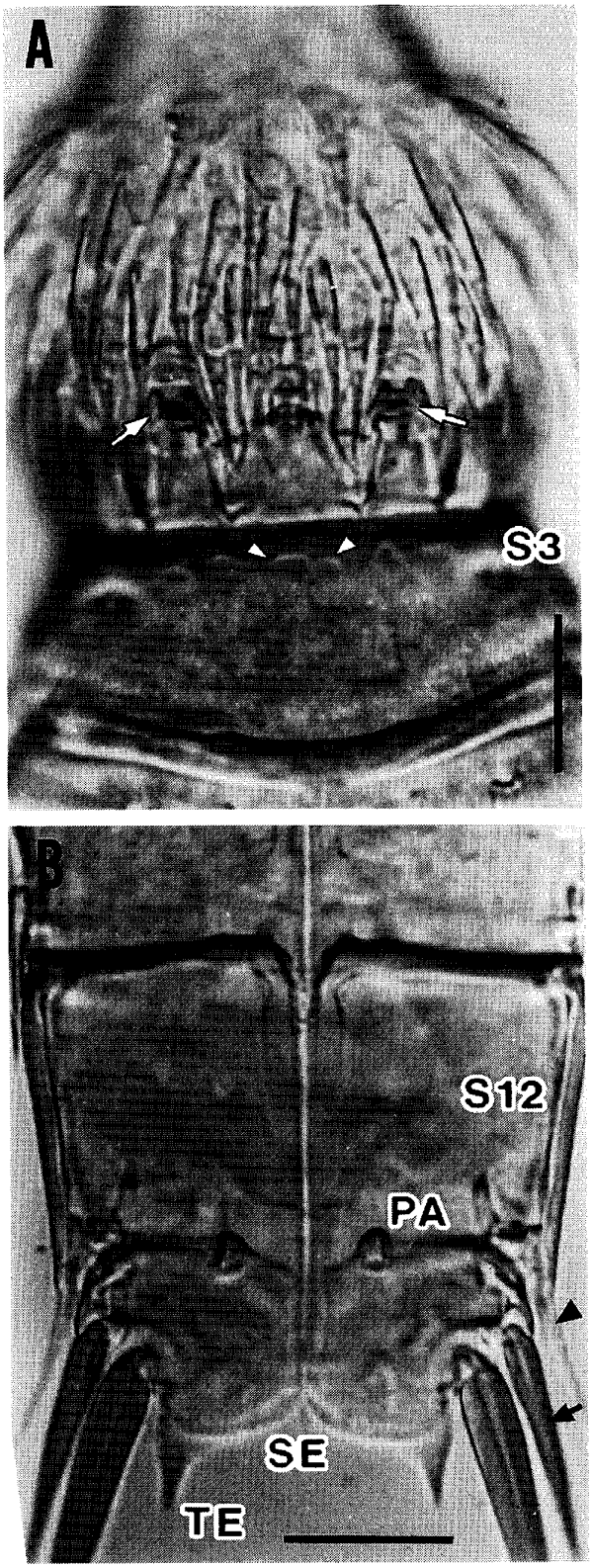

Fig. 6.

Segment 6: length 35 μm, maximum sternal width 56 μm, with middorsal spine 21 μm long, and with posterior pectinate fringe; otherwise similar to segment 5 except for presence of two additional pairs of sensory-glandular structures in paradorsal and dorsolateral positions.

Segment 7: length 39 μm, maximum sternal width 61 μm; middorsal spine 26 μm long; lateral spines/tubules 27 μm long; otherwise similar to segment 6 except for absence paradorsal and subdorsal sensory-glandular structures and presence additional pair of sensory-glandular structures in subventral position.

Segment 8: length 42 μm, maximum sternal width 63 μm; middorsal spine 29 μm long; lateral spines/tubules 21 μm long; muscle scars not prominent; otherwise similar to segment 7 except for absence of latter's middorsal and additional subventral sensory-glandular structures and presence of three additional pairs of sensory-glandular structures in paradorsal and subdorsal positions.

Segment 9: length 45 μm, maximum sternal width 64 μm; middorsal spine 32 μm long; lateral spines/tubules 26 μm long; midventral pachycycli with lateral incisions; one sensory-glandular structure in middorsal position; posterior pectinate fringe of cuticular elements well-developed; four pairs of sensory-glandular structures in paradorsal, dorsolateral, and subventral positions.

Segment 10: length 47 μm, maximum sternal width 66 μm; middorsal spine 35 μm long; lateral spines/tubules 30 μm long; otherwise similar to segment 9 except for absence of middorsal and one pair of subventral sensory-glandular structures.

Segment 11: length 48 μm, maximum sternal width 64 μm; lateral spines/tubules 32 μm long; midventral pachycycli with lateral incisions; two pairs of subdorsal and one pair of subventral sensory-glandular structures present; posterior pectinate fringe of cuticular elements well-developed.

Segment 12: length 53 μm, standard width 60 μm; lateral tubules 34 μm long, shifted to midlateral position (Fig. 6B, black arrowheads, for female); posterior pectinate fringe present; pair of large muscle scars in subdorsal position; three sensory-glandular structures in middorsal position; four pairs of sensory-glandular structures in subdorsal and subventral positions.

Segment 13: length 40 μm, maximum sternal width 45 μm, with deeply incised ventral pachycycli (Fig. 6B, PA, for female); tergal plate with prominent subdorsal pectinate fringe (Fig. 5B, PF) and subcuticular scar (Fig. 5B, arrowheads); terminal tergal extensions (Fig. 5B, TE) elongated, pointed, with mesial projection at base; terminal sternal extensions (Fig. 6B, SE, for female) nearly rounded, with slightly truncate appearance; sensory-glandular structure in middorsal position; lateral terminal spines 106 μm long, 38% of trunk length; two pairs of penile spines at arthrocorium between segments 12 and 13, PS-1 32 and PS-2 24 μm long, respectively.

Sexual difference. Males differing from females in having two pairs of long penile spines (PS), by slightly different arrangement of sensory-glandular structures and by shapes of terminal sternal extensions and pachycycli of segment 13 (Figs 2–3). In contrast to males, females with lateral accessory terminal spines (Fig. 6B, arrow) and slightly longer lateral tubules (Fig. 6B, black arrowhead) on segment 12 (Fig. 3). Females also differing from males by shape of large, subventral subcuticular scars on segment 3 (Fig. 6A, white arrowheads) and by less developed midventral articulation of segment 4 (Figs 2–4).

Table 1. Measurements (μm) and indices (%) for *Echinoderes aureus* adults

	Holotype male	Paratype males	Allotype female	Other paratype females
TL	277	297–313	313	294–313
MVP height	11	13	14	14
MVP width at top	6	6–7	10	10
MVP width at base	11	10–11	11	11–13
SVP height	13	13	13	13
SVP width at base	7	6–7	7	7
MDP height	13	13	14	14
MDP width at base	5	5	6	6
L-3	30	31	31	32
L-4	32	31–32	32	32–34
L-5	34	32	32	34
L-6	35	34	34	35–35
L-7	39	37	35	37–38
L-8	42	39–40	37	39–40
L-9	45	42–43	40	43–43
L-10	47	45–47	43	46–47
L-11	48	47–48	48	47–48
L-12	53	53–55	51	48–56
L-13	40	37–40	37	39–40
Anterior margin	56	56–58	60	56–61
MSW-5	47	48–50	50	45–48
MSW-6	56	56–58	60	58
MSW-7	61	60–63	64	61–63
MSW-7/TL (%)	22	20	21	20–21
MSW-8	63	63–66	68	65–67
MSW-9	64	64–68	69	66–68
MSW-10	66	64–66	68	68–69
MSW-11	64	63–63	66	64–69
SW	60	58–60	61	63–68
SW/TL (%)	21	19–20	20	20–23
MSW-13	45	43–47	48	48–51
DS-6	21	21	21	23–27
DS-7	26	24–27	26	24–29
DS-8	29	27–29	27	27–29
DS-9	32	31–32	32	32
DS-10	35	32–34	34	35
LS-4	29	29–32	32	27–31
LS-7	27	27	29	29
LS-8	21	19–23	23	21–23
LS-9	26	26	27	26–27
LS-10	30	29	29	31
LS-11	32	29–30	32	32
LS-12	34	31–32	39	39–39
LTS	106	98–103	103	103–113
LTS/TL (%)	38	31–35	33	35–36
LTAS			39	37–39
LTAS/TL (%)			12	12–13
LTAS/LTS (%)			38	33–38
PS-1	32	27		
PS-2	24	23		

Discussion

Fourteen valid species of *Echinoderes* have been described previously from the Pacific Ocean: *E. tchefouensis* Lou, 1934 from the Yellow Sea (northeastern China); *E. pennaki* Higgins, 1960 and *E. kozloffi* Higgins, 1977 from the San Juan Archipelago (northwestern USA); *E. newcaledoniensis* Higgins, 1967 from the southwestern Pacific (New Caledonia); *E. pacificus* Schmidt, 1974 from the eastern Pacific (Galapagos Islands); *E. nybakkeni* Higgins, 1986 from the coast of California; *E. filispinosus* Adrianov, 1989, *E. multisetosus* Adrianov, 1989, *E. koreanus* Adrianov in Adrianov and Malakhov, 1999, and *E. ulsanensis* Adrianov in Adrianov and Malakhov, 1999 from the Sea of Japan; *E. malakhovi* Adrianov in Adrianov and Malakhov, 1999 from New Zealand; *E. teretis* Brown in Adrianov and Malakhov, 1999; *E. cavernus* Sørensen, Jørgensen and Boesgaard, 2000 from Australia, and *E. sensibilis* Adrianov, Murakami and Shirayama, 2002 from Tanabe Bay in Japan.

Echinoderes masudai and *E. dujardinii* reported from the Pacific coast of the main islands of Japan (Abe 1930; Tokioka 1949; Sudzuki 1976a, b) are currently considered *species indeterminata* or misidentifications (Higgins 1983; Adrianov and Malakhov 1994, 1999) as explained in the Introduction. *Echinoderes dujardinii* is very common in European waters and was carefully re-described by Higgins (1977). *Echinoderes dujardinii* is easily distinguished from *E. aureus* n. sp. by the presence of lateral accessory spines on segment 10, terminal setae on pointed sternal extensions of segment 13, and shorter middorsal spines on segments 6–10.

In common with the new species, nine other Pacific species of *Echinoderes* have middorsal spines on segments 6–10. *Echinoderes koreanus* from Japan differs from *E. aureus* by the shape of the trichoscalid plates that are centered above the subventral and subdorsal placids, by the shape of the terminal tergal extensions on segment 13, and by the absence of lateral tubules on segment 4 (Adrianov and Malakhov 1999). In contrast to the new species, the second Korean species, *E. ulsanensis*, is characterized by remarkably short and thick lateral terminal spines and possesses lateral spines/tubules only on segments 8–10 (Adrianov and Malakhov 1999). *Echinoderes tchefouensis* is distinguished from the new species by the presence of lateral spines/tubules only on segments 7 and 10–11 (Lou 1934). In contrast to the new species, *E. pennaki* has no lateral tubules on segment 12 and possesses enlarged ventral pectinate fringes on segments 3–6 (Higgins 1960). *Echinoderes kozloffi* is easily distinguished from the new species in having sharp, slightly truncate sternal extensions with long terminal setae on segment 13 (Higgins 1977). In contrast to the new species, *Echinoderes nybakkeni* is characterized by remarkably long terminal lateral, terminal lateral accessory, middorsal, and lateral spines (Higgins 1986). The fourth species from the eastern Pacific, *E. pacificus*, differs from *E. aureus* in having sharp, truncate sternal extensions with long terminal setae on segment 13 and by the size of the middorsal spines, which are clearly longer than the corresponding segments (Schmidt 1974). *Echinoderes cavernus* is distinguished from the new species by the presence of very short middorsal spines on segments 6–10, remarkably short and thick lateral terminal spines, and rounded tergal extensions of segment 13 (Sørensen *et al.* 2000). The last Pacific species with middorsal spines on segments 6–10 is *E. sensibilis*, also described from the tide pools in Tanabe Bay in Japan. This species is characterized by the presence of remarkable trapezoidal fields of minute, cuticular hairs subventrally on segments

5–12. In addition, *E. sensibilis* differs from *E. aureus* in having very short middorsal spines about half as long as the corresponding segments (Adrianov *et al.* 2002).

Two species of *Echinoderes* from the northern part of the Sea of Japan, *E. multisetosus* and *E. filispinosus*, are well distinguished from the new species by the absence of middorsal spines (Adrianov and Malakhov 1999). In addition, *E. multisetosus* is characterized by the presence of large, oval, paradorsal fields of cuticular hairs on segments 6–11, accessory lateral spines on segments 9–10, and a pair of subventral tubules on segment 11, in addition to remarkably elongated and sharp terminal tergal extensions of segment 13 and lateral spines/tubules only on segments 7 and 10 (Adrianov and Malakhov 1999). The only other Pacific *Echinoderes* without middorsal spines is *E. malakhovi* (Adrianov and Malakhov 1999), which differs from *E. aureus* by the presence of large, subventral spines/tubules on segment 11. The most easily observed distinguishing feature of *E. teretis* is the presence of a single middorsal spine/tubule on segment 6 (Adrianov and Malakhov 1999). *Echinoderes newcaledonensis* is easily distinguished from the new species by the presence of remarkably long middorsal spines on segments 6, 8, and 10 (Higgins 1967).

Echinoderes aureus is distinguished from all other Pacific species by the presence of large subcuticular scars in a subventral position on segment 3 and the incomplete, weakly developed, midventral articulation on segment 4. The only other Pacific species with a slight indication of a sutured ventral midline is *E. nybakkeni*. A similar structure has been described for four species from Greenland: *Echinoderes angustus* Higgins and Kristensen, 1988, *E. aquilonius* Higgins and Kristensen, 1988, *E. eximus* Higgins and Kristensen, 1988, and *E. tubilak* Higgins and Kristensen, 1988 (see Higgins and Kristensen 1988). An incomplete midventral articulation of segment 4 has also been described for the genus *Cephalorhyncha* Adrianov, 1999 (in Adrianov and Malakhov 1999), but in contrast to *Echinoderes*, *Cephalorhyncha* also has complete ventrolateral articulations on segment 4.

Echinoderes aureus differs from all other Pacific species by the remarkable golden coloration of the cuticle in both living and fixed specimens. The color remains even in specimens mounted in Hoyer's medium after all internal organs have dissolved. Living specimens of *E. aureus* have a brownish yellow or yellow-greenish midgut and the contents can be seen clearly through the golden cuticle.

Echinoderes aureus is the fourth Pacific species described only from the intertidal zone. *Echinoderes kozloffi* was found in muddy sediments rich with detritus (Higgins 1977). *Echinoderes nybakkeni* was described from coars sand of a high-energy (Higgins 1986). *Echinoderes sensibilis* was found in washings of red algae, *Corralina pilulifera* Postele and Ruprecht, in tide pools (Adrianov *et al.* 2002); *E. aureus* is the first Pacific species found in washings of the intertidal brown algae *Padina arborescens*.

Key to Adults of *Echinoderes*

1. Middorsal spines (DS) present 2
– Middorsal spines (DS) absent 47
2. Middorsal spine (DS) single, short, on segment 6 only 3
– Middorsal spines (DS) on two or more trunk segments 5

3. Segment 4 remarkably swollen; spine-like ventral setae present on segment 10; lateral accessory spines (LAS) on segment 10; terminal sternal extensions (SE) without setae ..... *E. capitatus* (Zelinka, 1928) Karling, 1954
– Segment 4 not swollen; no spine-like ventral setae on segment 10; no LAS; SE each with long, lateral seta 4
4. Segment 4 with four pairs of spine-like tubules ..... *E. cantabricus* Pardos, Higgins and Benito, 1998
– Segment 4 lacking spine-like tubules or spines ..... *E. teretis* Brown in Adrianov and Malakhov, 1999
5. Middorsal spines (DS) on segments 6–10 6
– Middorsal spines (DS) absent on one or more of segments 6–10 34
6. Lateral spines/tubules (LS) on segment 6 ..... *E. agigens* Baçescu, 1968
– Lateral spines/tubules (LS) absent on segment 6 7
7. Lateral spines/tubules (LS) on segment 7 8
– Lateral spines/tubules (LS) absent on segment 7 55
8. Lateral accessory spines (LAS) on segment 10 9
– Lateral accessory spines (LAS) absent on segment 10 10
9. Middorsal spines (DS) very short, thick, tooth-like, 20–25% as long as corresponding segments ..... *E. gerardi* Higgins, 1978
– Middorsal spines (DS) about 50% (or more) of length of corresponding segments ..... *E. dujardinii* Claparède, 1863
10. Lateral spines/tubules (LS) on segment 4 (adhesive tubules) 11
– Lateral spines/tubules (LS) absent on segment 4 24
11. Lateral spines/tubules (LS) (or long setae in male) on segment 12 12
– Lateral spines/tubules (LS) or setae absent on segment 12 23
12. Terminal sternal extensions (SE) rounded, extending beyond short terminal extensions (TE); outer border of lateral terminal spines (LTS) denticulate ..... *E. krishnaswamyi* Higgins, 1985
– Terminal sternal extensions (SE) of other structure; outer border of lateral terminal spines (LTS) even 13
13. Midventral pachycycli (cuticular thickenings) of segment 5 remarkably wide; terminal tergite divided at midline ..... *E. nybakkeni* Higgins, 1986
– Midventral pachycycli (cuticular thickenings) of segment 5 not enlarged; terminal tergite not divided at midline 14
14. Middorsal spine (DS) on segment 10 twice as long as than DS on segment 9..... 15
– Middorsal spine (DS) on segment 10 equal in length or slightly longer than DS on segment 9 16
15. Lateral spines/tubules (LS) on segment 12 shortest, about half length of its segment; setae present near lateral spine on segment 12 of male ..... *E. ferrugineus* Zelinka, 1928
– Lateral spines/tubules (LS) on segment 12 longest, equal in length to its segment; no setae near lateral spines on segment 12 of male ..... *E. worthingi* Southern, 1914
16. Outer border of lateral terminal spines (LTS) serrulate along 1/3 of length; midventral pachycycli on segments 5–10 remarkably wide ..... *E. pilosus* Lang, 1949
– Outer border of lateral terminal spines (LTS) not serrulate; midventral pachycycli on segments 5–10 not wide 17
17. Lateral spines/tubules (LS) on segment 12 very short, about 30–50% as long as

other LS; seta near LS on segment 12 ..... *E. pacificus* Schmidt, 1974
– Lateral spines/tubules (LS) on segment 12 equal to or longer than other LS; no seta near LS on segment 12 18
18. Perforate sites absent ..... *E. imperforatus* Higgins, 1983
– Perforate sites present 19
19. Segments 5–12 with oval and trapezidal subventral fields of cuticular hairs; terminal sternal extensions (SE) without seta (caudate) ..... *E. sensibilis* Adrianov, Murakami and Shirayama, 2001
– Segments 5–12 without subventral fields of cuticular hairs; terminal sternal extensions (SE) each with terminal seta (caudate) extending beyond terminal tergal extensions (TE) 20
20. Segment 3 with two large, subcuticular scars in subventral position; segment 4 with incomplete, weakly developed, midventral articulation ..... *E. aureus* n. sp.
– Segment 3 without large, rounded subcuticular scars in subventral position; segment 4 without any articulations 21
21. Terminal sternal extensions (SE) rounded; middorsal spines (DS) shorter than corresponding segments ..... *E. ehlersi* Zelinka, 1913
– Terminal sternal extensions (SE) pointed; middorsal spines (DS) clearly longer than corresponding segments 22
22. Middorsal spines (DS) much longer than corresponding segments; DS-10 nearly equal to combined length of segments 11–12 ..... *E. sublicarum* Higgins, 1977
– Middorsal spines (DS) distinctly shorter than corresponding segments ..... *E. kozloffi* Higgins, 1977
23. Terminal tergal extensions (TE) sharp, slightly curved mesially, with thickenings at inner side; terminal sternal extensions (SE) rounded, with terminal spinose extension equal to TE ..... *E. brevicaudatus* Higgins, 1977
– Terminal tergal extensions (TE) rounded; terminal sternal extensions (SE) rounded, without spinose extension ..... *E. cavernus* Sørensen, Jørgensen and Boesgaard, 2000
24. Lateral spines/tubules (LS) or setae present on segment 12 25
– Lateral spines/tubules (LS) or setae absent on segment 12 27
25. Middorsal spine (DS) on segment 10 about twice as long as its segment; lateral spine/tubule (LS) of segment 12 equal to length of its segment..... *E. steineri* (Chitwood, 1951) Higgins, 1960
– Middorsal spine (DS) on segment 10 only slightly longer or shorter than its segment; lateral spine/tubule (LS) on segment 12 shorter than its segment 26
26. Lateral spines/tubules (LS) very short, distinctly shorter than corresponding segments; terminal sternal extensions (SE) truncate; no lateral setae on segment 13 ..... *E. truncatus* Higgins, 1983
– Lateral spines/tubules (LS), except for first one, not shorter than corresponding segments; terminal sternal extensions (SE) pointed; lateral setae present on segment 13 ..... *E. bookhouti* Higgins, 1964
27. Lateral spines/tubules (LS) on segments 7–11 28
– Lateral spines/tubules (LS) only on segments 7, 10, 11 33
28. Round pore or cuticular scar replacing lateral spine/tubule (LS) on segment 4; terminal sternal extensions (SE) rounded 29
– No round pore or cuticular scar at site of missing lateral spine/tubule (LS) on segment 4; terminal sternal extensions (SE) pointed .....

..... *E. remanei* (Blake, 1930) Karling, 1954

29. Ventral pectinate fringe (PF) of segment 3 composed of unequally long units, shorter on either side of midline ..... *E. tubilak* Higgins and Kristensen, 1988
– Ventral pectinate fringe (PF) of segment 3 composed of uniform units 30
30. Lateral terminal spines (LTS) short, only slightly longer than terminal accessory spines (LTAS), about equal to combined length of segments 12–13 ..... *E. aquilonius* Higgins and Kristensen, 1988
– Lateral terminal spines (LTS) more than twice as long as terminal accessory spines (LTAS), much longer than combined length of segments 11–13 31
31. Lateral terminal spines (LTS) very long, only slightly shorter than trunk length (LTS/TL 83%); terminal tergal extensions (TE) with distinct posteromesial interruption; lateral spines/tubules (LS) on segment 10 distinctly longer than LS on segment 11 ..... *E. stockmani* Adrianov in Adrianov and Malakhov, 1999
– Lateral terminal spines (LTS) less than 1/2 of trunk length (TL); TE without distinct mesial interruption; LS on segment 10 not longer than LS on segment 11 32
32. Combined length of ventral plates of segments 12 and 13 distinctly more than standard width (SW) of segment 12; ventral trichoscalid's plates roundish triangular, deeply incised anteriorly ..... *E. angustus* Higgins and Kristensen, 1988
– Combined length of ventral plates of segments 12 and 13 about equal to standard width of segment 12; ventral trichoscalid's plates remarkably short and wide, not incised ..... *E. pennaki* Higgins, 1960
33. Lateral spines/tubules (LS) on segment 10 dorsally displaced, not in line with other lateral spines; terminal tergal extensions (TE) pointed ..... *E. tchefouensis* Lou, 1934
– Lateral spines (LS) on segment 10 not dorsally displaced, in line with other lateral spines; terminal tergal extensions (TE) truncate terminally ..... *E. eximus* Higgins and Kristensen, 1988
34. Middorsal spines (DS) on two trunk segments only 35
– Middorsal spines (DS) on three or four trunk segments 36
35. Middorsal spines (DS) on segments 6 and 8; terminal tergal extensions (TE) long, pointed, mesially interrupted ..... *E. bispinosus* Higgins, 1982
– Middorsal spines (DS) on segments 6 and 9; terminal tergal extensions (TE) rounded ..... *E. citrinus* Zelinka, 1928
36. Middorsal spines (DS) on segments 6–9; lateral terminal accessory spines (LTAS) remarkably long, nearly equal to combined length of segments 11–13 ..... *E. setiger* Greeff, 1869 emend. Higgins, 1982
– Middorsal spines (DS) only on 3 trunk segments; LTAS much shorter than combined length of segments 11–13 37
37. Middorsal spines (DS) on segments 6, 7, 10 ..... *E. druxi* d'Hondt, 1973
– Middorsal spines (DS) on segments 6, 8, 10 38
38. Lateral spines/tubules (LS) present on segment 7 39
– Lateral spines/tubules (LS) absent on segment 7 ..... *E. arlis* Higgins, 1966
39. Lateral terminal spines (LTS) very short and thick, shorter than segment 12 ..... *E. abbreviatus* Higgins, 1983
– Lateral terminal spines (LTS) remarkably long, equal to combined length of at least 4 terminal segments 40
40. Lateral accessory spines (LAS) dorsally adjacent to lateral spines/tubules (LS)

on segment 10 41
– Lateral accessory spines (LAS) absent on segment 10.....
..... *E. bermudensis* Higgins, 1982
41. Subdorsal spines/tubules present on segment 4 42
– Subdorsal spines/tubules absent on segment 4 44
42. Segment 10 with two pairs of spines/tubules (LS and LAS) .....
..... *E. peterseni* Higgins and Kristensen, 1988
– Segment 10 with three pairs of spines/tubules in dorsolateral and lateral positions 43
43. Basal plates of subventral trichoscalids centered above subventral placids wide, incised anteriorly; terminal sternal extensions (SE) each with terminal seta ..... *E. hispanicus* Pardos, Higgins and Benito, 1998
– Basal plates of subventral trichoscalids centered above subventral placids narrow, nearly triangular, not incised; terminal sternal extensions (SE) lacking terminal setae ..... *E. newcaledoniensis* Higgins, 1967
44. Terminal tergal extensions (TE) sharply pointed, mesially interrupted or slightly concave, at least twice shorter than lateral terminal accessory spines (LTAS) 45
– Terminal tergal extensions (TE) remarkably long, with wide distal elements, equal in length to lateral terminal accessory spines (LTAS) .....
..... *E. higginsi* Huys and Coomans, 1989
45. Middorsal spines (DS) short, not longer than corresponding segments; subdorsal muscle scars (MS) absent on segment 4; terminal sternal extensions (SE) each with long terminal seta extending far beyond tergal extensions (TE) .....
..... *E. riedli* Higgins, 1966
– Middorsal spines (DS) much longer than corresponding segments; subdorsal muscle scars (MS) present on segment 4; terminal seta of SE, if present, not extending beyond TE 46
46. Middorsal spines (DS) more than twice as long as corresponding segments; DS-10 extending beyond posterior margin of segment 12; terminal sternal extensions (SE) each with terminal seta ..... *E. kristenseni* Higgins, 1985
– Middorsal spines (DS), except for DS-10, less than twice as long as corresponding segments; DS-10 not extending beyond posterior margin of segment 12; terminal sternal extensions (SE) without terminal setae .....
..... *E. wallaceae* Higgins, 1983
47. Segment 11 with two ventral spine-like setae/tubules 48
– Segment 11 lacking ventral spine-like setae/tubules 49
48. Segment 4 very short, no more than 40% as long as segment 3; lateral spines/tubules (LS) absent on segment 12; lateral accessory spines (LAS) present on segments 9–10; lateral terminal accessory spines (LTAS) robust, curved mesially ..... *E. multisetosus* Adrianov, 1989
– Segment 4 over half as long as segment 3; LS present on segment 12; LAS absent; LTAS not curved mesially ..... *E. malakhovi* Adrianov, 1999
49. Lateral spines/tubules (LS) present on segment 4; female with lateral terminal accessory spines (LTAS) 50
– Lateral spines/tubules (LS) absent on segment 4; female without lateral terminal accessory spines (LTAS) 51
50. Lateral accessory spines (LAS) present on segment 10 ..... *E. horni* Higgins, 1983

– Lateral accessory spines (LAS) absent on segment 10 ..... *E. andamanensis* Higgins and Rao, 1979

51. Lateral spines/tubules (LS) present on segment 11 ..... *E. caribbiensis* Kristeuer, 1964
– Lateral spines/tubules (LS) absent on segment 11 or replaced by minute seta 52
52. Lateral terminal spines (LTS) longer than 1/2 of trunk length (TL) 53
– Lateral terminal spines (LTS) shorter than 1/3 of trunk length (TL) 54
53. Lateral spines/tubules (LS) on segments 7 and 10 equal in length; two dorsolateral spine-like, sensory elements present at posterior border of segment 12 ..... *E. filispinosus* Adrianov, 1989
– Lateral spines/tubules (LS) on segment 7 half as long as LS on segment 10; no dorsolateral spine-like elements at posterior border of segment 12 ..... *E. maxwelli* (Omer-Cooper, 1957) Higgins, 1960
54. Lateral spines/tubules (LS) on segments 7 and 10 distinct, long (about 30 μm in length) ..... *E. bengalensis* (Timm, 1958) Higgins, 1960
– Lateral spines/tubules (LS) on segments 7 and 10 underdeveloped, present as minute setae ..... *E. coulli* Higgins, 1977
55. Lateral spines/tubules (LS) present on segment 8; lateral terminal spines (LTS) about 1/2 of trunk length (TL) or shorter 56
– Lateral spines/tubules (LS) absent on segment 8; lateral terminal spines (LTS) very long, nearly equal to trunk length (TL) ..... *E. levanderi* Karling, 1954
56. Lateral terminal spines (LTS) remarkably short and thick, distinctly shorter than segment 12, about 11% of trunk length (TL) ..... *E. ulsanensis* Adrianov in Adrianov and Malakhov, 1999
– Lateral terminal spines (LTS) much longer than segment 12, about 25–50% of trunk length (TL) 57
57. Subdorsal spine-like setae/tubules present on segments 9 and 11 ..... *E. koreanus* Adrianov in Adrianov and Malakhov, 1999
– Subdorsal spine-like setae/tubules absent 58
58. Lateral terminal spines (LTS) less than 1/2 of trunk length (LTS/TL 25–40%); lateral terminal accessory spines (LTAS) nearly equal in length to segment 12 ... *E. svetlanae* Adrianov in Adrianov and Malakhov, 1999
– Lateral terminal spines (LTS) nearly equal to 1/2 of trunk length (LTS/TL 50%); lateral terminal accessory spines (LTAS) nearly equal to combined length of segments 12–13 ..... *E. elongatus* (Nyholm, 1947) Karling, 1954

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